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Aspects of Life History and of Territorial Behavior in Young Individuals of *Platynereis bicanaliculata* and *Nereis vexillosa* (Annelida, Polychaeta)[1]

PAMELA ROE[2]

ABSTRACT: *Platynereis bicanaliculata* (Baird), an annual nereid, spawned in early August at two areas in Washington state. Spawning was highly synchronous. Young were planktonic for about 1 week. Within 3 weeks they had grown to 4 mm in length, had started building tubes of mucus and diatoms, and showed a period of rapid growth in size. By the end of September or early October they averaged 10 mm in length, at which size they remained until March. In spring they reached adult length (20–23 mm) and during the summer gametes developed.

Nereis vexillosa Grube egg masses were found from March through August. *Nereis* has a 2-year life span in both study areas, growing to one-half adult size the 1st year and to mature size the 2nd year. In the laboratory, young made tubes within 1 week after hatching from egg masses.

Members of both species defend their tubes from intruders. Usually, larger individuals win fighting encounters, especially if they are the occupants of tubes. Small individuals successfully defend their tubes from larger individuals in about one-half of the encounters; and if fights occur between equal sized individuals, occupants are usually not displaced. Fights are real, with jaws used much for biting, and smaller individuals are sometimes actually eaten by larger ones, especially in *Nereis vexillosa*. In the laboratory the number of individuals of *N. vexillosa* kept in fingerbowls decreased in number until only one or two large individuals remained.

NEREIDS can be abundant and important members of intertidal mud flat communities (Roe 1971, Woodin 1974). This paper describes territorial behavior in newly settled young and compares life history and territorial behavior in two species, *Platynereis bicanaliculata* (Baird) and *Nereis vexillosa* Grube. Territorial behavior of several nereid species has been studied in the laboratory (e.g., Reish and Alosi 1968, Evans 1973) using fully grown but usually nonripe animals. This is the first description of such behavior in newly settled nereids. The adaptive significance of this territorial behavior, evident even before young animals have commenced feeding, is discussed, and the effect of nereid territorial behavior on mud flat community structure is suggested.

MATERIALS AND METHODS

Nereids were studied from two intertidal mud flats on San Juan Island, Washington: one at Mitchell Bay (48°34′9.5″ N, 123°9′48″ W) and one at Garrison Bay (48°34′57″ N, 123°9′17″ W). At Mitchell Bay ulvoids were abundant and patches of these algae remained throughout the year. At Garrison Bay ulvoids were present in spring and summer, but were absent throughout winter; other algae were also scarce then. The Mitchell Bay area had some coarse sand and gravel; the Garrison Bay site was soft mud over a hard-packed clay.

Platynereis bicanaliculata was collected in alternate months at the two areas. A primary transect was laid high in the intertidal; at 20-m

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[2] California State College, Stanislaus, Department of Biological Sciences, 800 Monte Vista Avenue, Turlock, California 95380.

22-2

intervals along this transect, transects perpendicular to it and leading to the lower intertidal were laid, and every 10 m along these secondary transects a wooden 1 m^2 quadrat was placed. A jar with a surface area at the opening of 20 cm^2, inverted and pressed into the mud in the center of the quadrat, was used to collect mud. During summer when nereids were larger and less abundant, plastic freezer boxes with a surface area of 100 cm^2 were used. In the laboratory, contents of each container were emptied with sea water into a Pyrex dish and sloshed around until all nereids swam to the water surface. They were counted, and nereids from the samples with the most individuals were preserved in 70-percent ethyl alcohol and their lengths were later measured for size frequency analysis.

Nereis vexillosa was collected in 1/8 m^2 samples of sieved mud from both areas in alternate months. Individuals were measured only 1 month, but casual observations of the sizes of other specimens support data for that month.

Egg masses of *Nereis vexillosa* were brought from both study areas to the Friday Harbor Laboratories, placed in fingerbowls in running sea water (about 10° C), and observed.

Platynereis trochophores collected from the plankton of Mitchell and Garrison bays were kept in fingerbowls in running sea water (10° C) and observed. All observations of territorial behavior were made in the laboratory, with young nereids in 4.5-inch (11.4 cm) diameter fingerbowls being used.

Sizes of newly hatched nereids usually were recorded as how many segments had grown rather than by actual size.

During fall and winter nereids were held in 4- or 16-ounce jars in a refrigerator kept near 7° C.

Young nereids were fed diatoms that grew on the sides of the running seawater tanks; in fall and winter they were fed fresh or dried ulvoids broken into small pieces. Growth and behavior were recorded.

The work by Berkeley and Berkeley (1948) was used to identify *Nereis vexillosa*; Hartman's work (1954) was used for *Platynereis bicanaliculata*.

OBSERVATIONS AND RESULTS

Life History of Platynereis bicanaliculata *(Baird, 1863)*

Platynereis is an annual; thousands of small eggs (132 μ in diameter) are spawned by each female into the open water, and, after spawning, both sexes, which have formed epitokal breeding swarms, die. Spawning is highly synchronous; I observed nearly all individuals of the *P. bicanaliculata* population at Mitchell Bay swarming and spawning gametes near midnight on 3 August 1969, and I observed the beginning of epitokal swarming at 2230 hours on 31 July 1968. Much of the *Platynereis* population at Garrison Bay spawned the same nights in 1968 and 1969 as did the Mitchell Bay population, as evidenced by the very large numbers of gastrulae that I observed in the plankton of both areas on 4 August 1969. That spawning is highly synchronous is evidenced by the fact that I saw only nine individuals swimming on 29 July 1969 (2300–2330 hours) and only 17 on 1–2 August 1969 (2230–0015 hours) at Mitchell Bay.

At both places there were minor spawning periods in late June and mid-July: I observed a much smaller number of nereid gastrulae or three-segmented larvae in plankton samples from Garrison Bay on 11 July 1969 and on 19 July 1969 from Mitchell Bay. I also observed a few *P. bicanaliculata* males swimming as if in breeding swarms on 24 June 1969 and 10 July 1969 at Mitchell Bay. However, compared to the enormous numbers of swarming adults seen on 31 July–1 August 1968 and 3 August 1969, and compared to the great number of gastrulae seen in plankton samples on 4 August 1969, the number of adults that spawned earlier constituted only a small portion. Guberlet (1933) reported highly synchronous swarms of *Platynereis* at Friday Harbor in June–August 1929–1932; so this synchronous, massive swarming behavior appears to be predictable. That animals die soon after spawning is evidenced by the fact that I could find very few large individuals of *P. bicanaliculata* at either study area by 23 August; at both places tiny, 4–5 segment individuals were then abundant in algae. On 14 July 1969, in contrast, there was an average of 75 large individuals (in 20 samples, standard error = 27.98) per square meter at Mitchell Bay. There is nearly a complete turnover of the population every August, although a few adults spawn (and die) in June and July and a few have not spawned by August.

Development and Behavior

Within 1 day eggs cultured in the laboratory at 10° C are swimming gastrulae and within 2 days have become trochophores. The trochophores have lipid droplets and larvae do not feed until they become benthic. In 7 to 8 days they have three segments and more or less rest on the bottom, although they do swim up into the water column at the least disturbance. (Guberlet, 1933, reported the beginning of three segments in 80 hours.) In the laboratory the small nereids started feeding on diatoms before 17 days, when they had four segments. By 1 month's time they had eight plus segments, were about 2 mm long, and had built mucous and diatom houses. In nature (Mitchell Bay and Garrison Bay) they settled out of the plankton within 3 weeks at four segments or less. Most settled in young ulvoids, seeming to prefer algae to sand.

Counts were not made of the number of eggs produced per female or the number surviving to trochophore, but there were averages of 6021 (in 23 samples, standard error = 1968) and 7000 (in 11 samples, standard error = 2969) small individuals of *P. bicanaliculata* per m^2 at Mitchell Bay in September 1968 and October 1969, respectively, and averages of 2750 (in 10 samples, standard error = 901) and 3500 (in four samples, standard error = 2179) per m^2 at Garrison Bay in October 1968 and 1969 (Roe, unpublished data).

The size-frequency histogram (Figure 1) for Mitchell Bay (see Roe 1971 for the similar Garrison Bay population) suggests two periods of rapid growth by *P. bicanaliculata*: in August–September after settlement and in April–May. After settlement, young worms grow to a length of about 10 mm by the end of September. They stay an average of 10–12 mm from then until mid-March. In March new ulvoids start growing on the mud flats and *P. bicanaliculata* individuals again grow rapidly (see also the following experiment). During summer the nereids do not grow in length, but rather develop gametes and become epitokous for spawning. Their diameters increase greatly during this time.

In April and May 1969, individuals of *P. bicanaliculata* were kept in four fingerbowls; five large (about 45 mm long) or 10 small (15–20 mm long) worms per bowl. Four pieces of ulvoids, cut into 7.5 × 3 cm rectangles, were added as food to each bowl when it became empty. The 10 larger worms ate the algae faster than did the 20 small ones, even though the latter were twice as many. The five large nereids eating the thinner-bladed ulvoid ate all of it, except for what they used as houses, in an average of 4 days; the others ate somewhat slower. The small worms ate so slowly that the algae grew considerably; so accurate measurements of the amount they ate were not made.

The 10 large worms grew from $\bar{x}$ 80 mg weight/worm to $\bar{x}$ 130 mg/worm in 12 days (five animals weighed together and total divided by 5 each time showed five animals weighing 79.3 mg and five weighing 81.3 mg on 2 May; five weighing 128.93 mg and five weighing 130.79 mg on 14 May).

The rapid growth rate in nature in spring was first attributed to growth of young algae on the mud flats. However, this is not the only reason for rapid growth by *P. bicanaliculata* then. During the fall, winter, and spring of 1969 and 1970, I kept some young individuals in the laboratory at 7° C, feeding them on *Enteromorpha* that I had collected at Mitchell Bay in October and then dried. The nereids grew hardly at all though winter. In April, I divided these nereids into two groups, feeding one-half on young spring *Enteromorpha* and one-half on the dried *Enteromorpha*. Nereids collected in the field in March that were the same size (average length = 1.5 cm) as those used in the experiment were used as controls and were not fed. Some nereids fed on the young, fresh alga died after 7 weeks, but they had grown to an average length of 5 cm before they died. The ones fed on dried *Enteromorpha* grew faster than they had all winter (to an average length of 2.5 cm in 11 weeks). The unfed controls did not grow during the duration of the experiment. The individuals fed fresh algae grew faster than those fed dried food, but those fed dried food

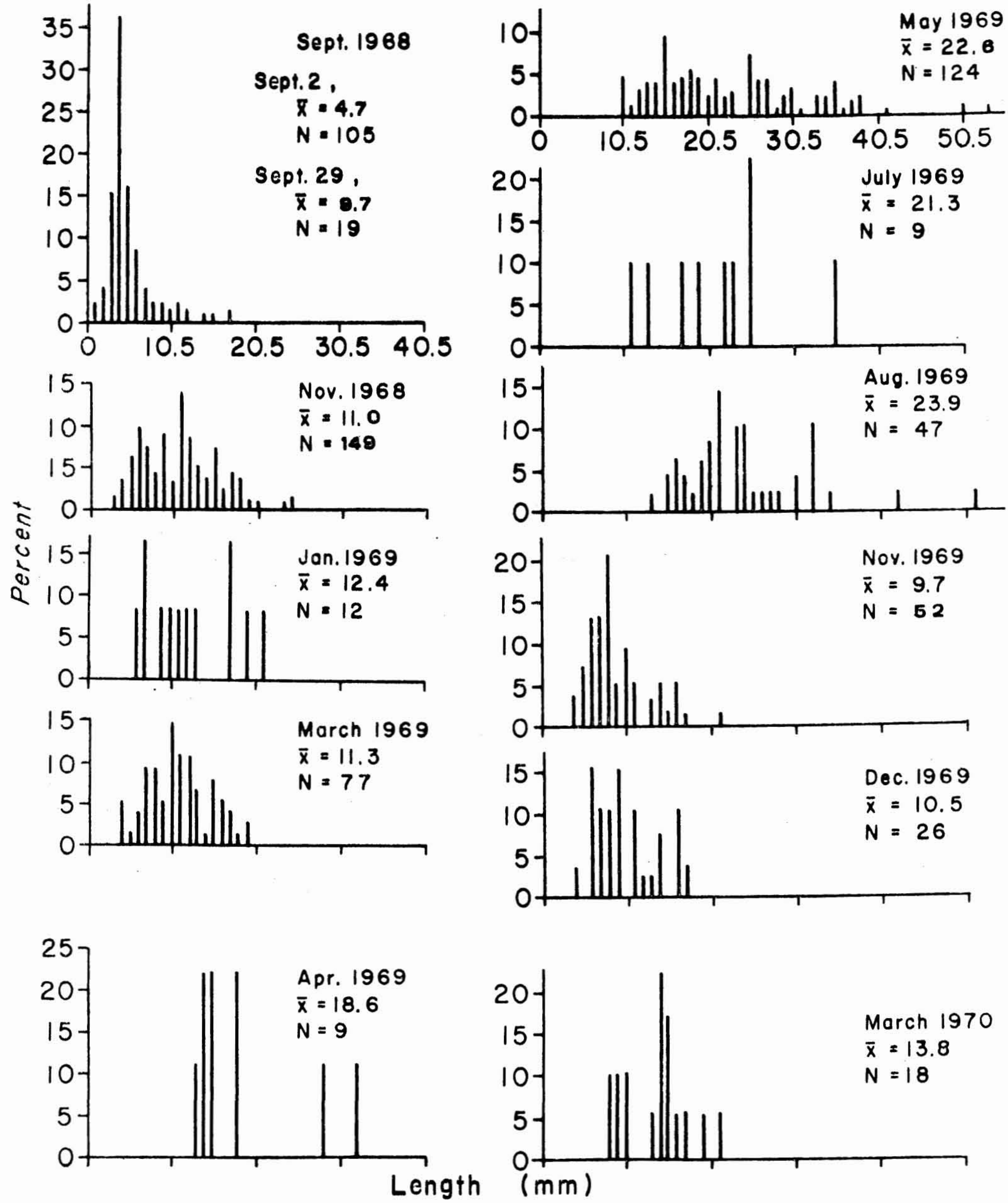

FIGURE 1. Size-frequency distribution of the Mitchell Bay *Platynereis bicanaliculata* population, September 1968–March 1970. $\bar{x}$ = average size of individuals in the population. N = number in sample.

grew faster than they had on the same dried food all winter. So it appears that an internal timing mechanism for growth plus a new crop of algal food in the spring are both factors in the rapid growth of *P. bicanaliculata* individuals in spring.

Population Aspects of Nereis vexillosa *Grube, 1849*

Nereis vexillosa is the other common nereid at Mitchell and Garrison bays. At both areas individuals of this species appear to have a 2-

year life span. In May 1969, 36 nereids measured fell into three major size classes, with eight being 3.5–5.5 cm in length, 16 being 6.5–9.5 cm, and 13 being 10.0–13.0 cm long. Young individuals kept in the laboratory from April to November grew to 4.5 and 6 cm, respectively. These data indicate that individuals of this species grow to about one-half adult size their 1st year and to adult size their 2nd year, during which spring or summer they become epitokous, spawn, and die. (They can, however, spawn at the end of their 1st year. See Johnson 1943.)

Egg masses lying on the surface of the mud were observed by Roe and Woodin (personal communication) between 10 March and 30 July at Mitchell Bay; egg masses were observed by Roe at Garrison Bay from late April through 23 August. The breeding season is long and asynchronous in both areas.

Eggs are laid in jelly clumps (see Johnson 1943 for picture), individual eggs being about 250 μ in diameter. Small worms hatch from the egg masses at the three-segment stage, about 0.322 mm in length, after 3 to 4 days in the laboratory. They swim rather than crawl until the four- to five-segment stage (about 1 week in the laboratory). Within that week they make tubes from mucus and diatoms and then are mainly benthic. After 3.5 weeks they range from 8 to 25 segments and 0.7 mm to 5.5 mm in length, with some individuals growing more rapidly than others.

Settlement, Tube Building, and Tube Defense

The following refers both to *Platynereis bicanaliculata* and to *Nereis vexillosa*, although most reported observations were on *Nereis* since it is a more benthic species early in its life and, therefore, easier to observe; the same observations were made using *P. bicanaliculata* individuals (see also Woodin 1974), although such observations on *Platynereis* were fewer in number. All observations of tube building and territorial behavior were made on individuals in 4.5-inch fingerbowls, usually with a dissecting microscope.

When small nereids settle out of the plankton they build mucous tubes to live in. They stay within the tubes, going partway out the front end and biting off algae, grabbing diatoms, etc., to add to the outside of the tube, anterior end first. *Nereis vexillosa* makes a tube within 1 week of hatching from the egg mass, at the four- to five-segment stage. *Platynereis bicanaliculata* individuals start making tubes at four to five segments also, but they do not make tubes that completely cover them until after they reach six segments in length. Earlier than six segments, they spend much time under anything available (clumps of diatoms, sand grains, etc.). The ratio of tube length to worm length in *N. vexillosa* averaged 1.65:1 (four measurements, range = 4:1 to 1.4:1); tubes of *P. bicanaliculata* were also longer than the animals but were not measured in this study.

Individuals defend their tubes against other individuals of the same species. Defense is of a small territory—of a circle at both openings of the tube; i.e., another nereid can build a tube overlying the first and there will be no conflict if doorways do not meet. Few measurements were obtained of the length of worm exposed at the entrance to a tube compared with the total length of the same worm, but nereids measured tended to be positioned with about one-half of the body out of the tube (9:19 mm and 13:25 mm exposed in two measurements), although sometimes most of the worm was exposed (22:23 mm exposed, one measurement). The ratio of total tube length to length of animal exposed averaged 2.52:1 in 10 measurements (range = 6.4:1 to 1.7:1). Assuming the exposed length of the nereid equals the diameter of the circle most often defended at each end of the tube (and from observation this does seem to be the case), then the diameter of this circle is about 2.5 times smaller than the length of the tube and is about one-half the length of the occupant.

In laboratory fingerbowls, nereid defense of tube and territory involves fighting (as described for adult nereids in Reish and Alosi 1968) and is important in keeping them; a worm that loses a fight is displaced and has to win or build another tube. It was observed that larger individuals almost always win fights and keep their tubes when smaller individuals without tubes fight them (five of five battles won). In fights between worms of equal sizes, individuals usually win and keep their tubes from intruders

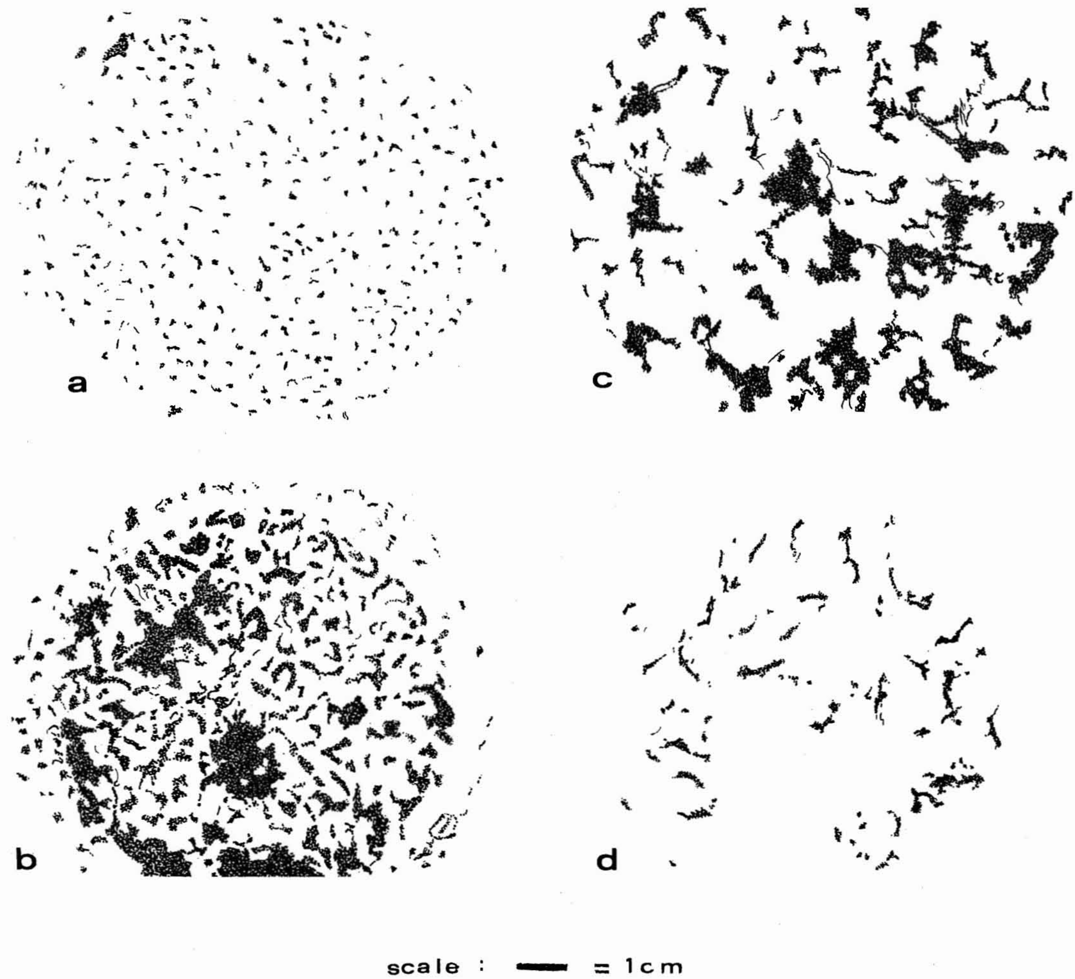

FIGURE 2. Drawings from photographs of distribution of diatom and mucous tubes of young nereids in finger-bowls. Some tubes were built a short way up the sides of the dishes. *a*, Tubes of *Nereis vexillosa*, about 2 weeks after hatching; *b*, tubes of a second group of *Nereis vexillosa*, about 3 weeks after hatching; *c*, tubes of *Nereis vexillosa* seen in *a*, about 1 month after hatching; *d*, tubes of 6-week-old *Platynereis bicanaliculata*.

(five of seven fights), but occasionally are displaced (two of seven fights). Small individuals with tubes win over larger worms without tubes about one-half the time (small won five times and lost five times in 10 episodes). Wins and losses occur when fights are at the front or the rear of a tube. If an intruder tries to displace an occupant from the rear, the occupant often turns around in its tube and fights.

Nereis vexillosa starts making and defending tubes even before the lipid food reserves of the egg are gone. It does not start to feed until later (at the five- to six-segment stage, about 10 days after hatching). Before they are five segments long, individuals show increased activity but not aggression when approached by others; but within 2 weeks of hatching (seven–eight segments), they have become highly territorial, with much fighting occurring between individuals in fingerbowls in the laboratory. From observations of animals from the same egg mass, I saw that unequal growth rates occur among individuals; the fast growers made tubes first, usually defended them better, and grew at increasingly rapid rates compared to slower individuals. The smaller worms become progressively worse off and, among *Nereis vexillosa* (but not observed with *P. bicanaliculata*), I have seen larger worms actually eat smaller losers of fights. This differential growth was also noticed by Johnson (1943) although he did not comment on its significance. High numbers of *Nereis* hatch from egg masses, but *Nereis* density is rather low (about 22/m^2 average at Mitchell Bay [Roe 1971]). Spacing and high mortality may be due in part to negative intraspecific interactions. In laboratory fingerbowls from 22 April to 1 June there was a strikingly even distribution of nereid tubes (Figure 2*a–c*) and the number of tubes decreased from about 350 to about 65 (Figure 2*a–c*). Tubes also became larger and spaced further apart during this time. By November, in three containers only one (two jars) or two (one jar) large nereids remained. The smaller ones presumably had been eaten inasmuch as no carcasses were found.

Platynereis bicanaliculata seems somewhat less aggressive, with territorial fighting well developed by 20 segments or so. Even spacing of tubes was observed (Figure 2*d*), but individuals were not seen eating others and many worms of this species can be kept together in 4-ounce jars for months.

Once a tube is made, a nereid usually comes only partway out to snatch a clump of algae and drag it back into the tube to eat it; a worm will leave the tube (in the laboratory) only when food is too far away to reach otherwise. If an individual is thus forced out of its tube, when it returns it will enter any vacant tube, not necessarily the one it left.

DISCUSSION AND CONCLUSIONS

The life histories of the common nereids on two mud flats in Washington are quite different: *Platynereis bicanaliculata*, the smaller of the two, is an annual with highly synchronous spawning and planktonic trochophores. *Nereis vexillosa* has a 2-year life span, and members of a population shed eggs from March through August. Eggs are in benthic jelly masses and the young are predominately benthic upon hatching. However, behaviors of the two nereids are remarkably similar. In both species, soon after the young become benthic they start building tubes of mucus and any available materials (in this study, diatoms), and they defend these tubes from intruders. This behavior has been studied in several species of adult nereids by Reish and Alosi (1968) and by Evans (1973) and is widespread throughout the family.

Territorial behavior and defense of tubes also occurs in very young worms soon after they have become benthic. In one species (*Nereis vexillosa*) tube building and defense begins even before the worms begin feeding. A behavioral pattern that begins so early and continues throughout the life of an individual must be adaptive for the individual. Although the adaptive significance of territorial behavior and tube defense is not known for nereids, several possibilities come to mind. Remaining in one's tube as an antipredator strategy is possibly one major adaptively significant aspect of this behavior. The nemertean *Paranemertes peregrina* ate anywhere from 14 to 35 percent of the nereid populations at the areas studied (Roe, unpublished data). *Paranemertes peregrina* appeared to take longer to locate a nereid if the nereid remained in its tube.

Maintaining a tube with algae on the outside surface also ensures a close food supply for a nereid as the attached algae grows (Woodin 1974). Woodin (1974) has shown that nereids thus actually farm algae.

Woodin (1974) has also shown that *Platynereis bicanaliculata* is competitively dominant to other polychaetes, such as *Armandia brevis* and *Axiothella rubrocincta*, and territorial behavior may be involved. Further studies in nature should be carried out to see if *P. bicanaliculata* uses territorial behavior against *A. brevis* as a means of maintaining its competitive dominance for space. I did not study interspecific aggression, but Reish and Alosi (1968) reported it among some nereid species, and Evans (1973) reported that interspecific aggression is stronger than intraspecific in some nereid species. It is certainly important in intraspecific competition for space, as this study with *Nereis vexillosa* shows.

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